Outflying climate change

Optimal timing of migratory geese breeding in a warming Arctic

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CHAPTER 2

Forage plants of an Arctic-nesting herbivore show larger warming response in breeding than wintering grounds, potentially disrupting migration phenology

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ABSTRACT

During spring migration herbivorous waterfowl breeding in the Arctic depend on peaks in the supply of nitrogen-rich forage plants, following a 'green wave' of grass growth along their flyway to fuel migration and reproduction. The effects of climate warming on forage plant growth are expected to be larger at the Arctic breeding grounds than in temperate wintering grounds, potentially disrupting this green wave and causing waterfowl to mistime their arrival on the breeding grounds. We studied the potential effect of climate warming on timing of food peaks along the migratory flyway of the Russian population of barnacle geese using a warming experiment with open-top chambers. We measured the effect of 1.0-1.7 °C experimental warming on forage plant biomass and nitrogen concentration at three sites along the migratory flyway (temperate wintering site, temperate spring stopover site and Arctic breeding site) during two months for two consecutive years. We found that experimental warming increased biomass accumulation and sped up the decline in nitrogen concentration of forage plants at the Arctic breeding site but not at temperate wintering and stop-over sites. Increasing spring temperatures in the Arctic will thus shorten the food peak of nitrogen rich forage at the breeding grounds. Our results further suggest an advance of the local food peak under 1-2°C climate warming, which will likely cause migrating geese to mistime their arrival at the breeding grounds, particularly considering the Arctic warms faster than the temperate regions. The combination of a shorter food peak and mistimed arrival, is likely to decrease goose reproductive success under climate warming by reducing growth and survival of goslings after hatching.

Introduction

The matching of animal's annual cycles to peaks in food availability is considered to be an important adaptation for successful reproduction (Lack 1968). A multitude of species match their period of reproduction to peaks in food availability in order to feed their young and to maximize their growth rates (Both & Visser 2005). During spring migration, migratory species can also travel along a climatic gradient and match arrival on stopover sites to local peaks of food abundance along the gradient, described as the 'green wave hypothesis' (Drent et al. 1978; van der Graaf et al. 2006; Shariatinajafabadi et al. 2014; Thorup et al. 2017). This strategy is especially important for species which partly rely on capital body stores accumulated at staging sites for egg formation and incubation, such as geese (Gauthier et al. 2003; Drent et al. 2007; Hahn et al. 2011). The matching of migration timing to peaks in food availbillity could be strongly disrupted by global climate warming when food peaks change asynchronously over the migratory flyway (Klaassen et al. 2012).

Global climate warming has advanced the phenology of spring events, such as the leafing and flowering of trees and emergence of insects (Visser & Both 2005; Menzel et al. 2006; Parmesan & Yohe 2003). Several bird species have been able to advance their laying date accordingly (Visser & Both 2005), while others, notably long-distance migrants, have not (Clausen & Clausen 2013; Møller et al. 2008; Both & Visser 2001). Such a mismatch in intertrophic relationships can have large consequences for reproductive success and, ultimately, population size (Both & Visser 2001; Miller-Rushing et al. 2010; van Gils et al. 2016; Møller et al. 2008). Migratory species are more vulnerable to these mismatches, as changes in climate are often not correlated between their wintering sites and breeding grounds (Kölzsch et al. 2015; Emmenegger et al. 2016). In the Arctic region climate warming is expected to be more severe than the global average, a process called arctic amplification (Stocker et al. 2013; Serreze et al. 2009), and rapid advancement of the onset of spring inducing strong phenological responses of plants and animals are already found in the Arctic (Høye et al. 2007; Post et al. 2009). Accelerated warming in the Arctic is expected to cause food peaks in Arctic regions to advance at a faster rate than in temperate regions, which could cause mismatches especially for Arctic long distance migrants (McKinnon et al. 2012).

Arctic long distance migrants, such as geese, take benefit from both temperate and Arctic food peaks to maximize reproductive success, by using the food peaks in temperate regions to fuel migratory flight, egg production and incubation (Drent et al. 2007) and the food peak in the Arctic to rear their chicks (van der Graaf et al. 2006; Doiron et al. 2015). As food peaks along the migratory flyway match the onset of spring (Van Der Graaf et al. 2006; van Eerden et al. 2005), geese use these to time their migration (Duriez et al. 2009; Shariatinajafabadi et al. 2014; van Wijk et al. 2012). Food peak phenology

might be differentially affected by climate warming at different latitudes, as plants in colder, higher latitudes might be more responsive to temperature increase (Havström et al. 1993). When food peaks along the flyway advance at different rates this can affect migration and reproduction of Arctic nesting geese in two ways: 1) When food peaks in the Arctic advance faster than in temperate regions, the period between the food peaks in temperate zones and the food peak on the breeding grounds becomes shorter. This may make it more difficult for the geese to benefit from multiple food peaks along a green wave (van der Graaf et al. 2006), causing them to arrive on the breeding grounds either later or with less body stores to initiate breeding. 2) When food peaks in the Arctic and in temperate regions advance at different rates, the cues which the geese currently use to time their departure might prove to be no longer valid (McNamara et al. 2011; Emmenegger et al. 2016). Geese will then suffer from reduced capacity to predict an earlier peak at the Arctic site and arrive too late (Kölzsch et al. 2015).

Already now, some Arctic nesting geese have been found to initiate nesting too late under increased spring temperatures in the Arctic, resulting in a mismatch between hatching date and high quality food availability (Dickey et al. 2008), reducing gosling growth rates (Doiron et al. 2015) and possibly driving declines in reproductive success (Clausen & Clausen 2013). As Arctic food peaks are predicted to advance under increasing temperatures (Doiron et al. 2014) these mismatches will likely become stronger under amplified climate warming in the Arctic (Doiron et al. 2014; Doiron et al. 2015). However, as food peak phenology might be differentially affected at different latitudes, it is currently unclear how an advancement of food peaks in the Arctic relates to advancement of food peaks along the migratory flyway, and thus whether it can lead to a mismatch of migratory timing. In order to make predictions on the extent of such a mismatch it is necessary to study how food peaks along the complete migratory flyway will advance under predicted climate change.

We studied the potential effect of climate warming on the advancement of food peaks along the migratory flyway of an Arctic nesting goose. We examined the impact of experimental warming on forage plant biomass, nitrogen concentration and peak nitrogen availability, using open top chambers at a wintering, staging and breeding site. We then apply the empirically determined relationship between growing degree days, i.e. the sum of mean daily temperatures above a certain temperature threshold (van Wijk et al. 2012), and nitrogen / nitrogen concentration to calculate the potential advancement of food peaks under 1 to 2°C climate warming. We specifically test the hypothesis that climate warming advances food peaks more in the Arctic breeding site than in temperate wintering and stopover sites, thus shortening the period between subsequent food peaks along the migratory flyway.

Methods

Study system and study sites

As a study system we used the migratory flyway of the Russian population of barnacle geese *Branta leucopsis*, which stretches between their wintering areas in North-Western Europe, along the Baltic Sea and White Sea to the breeding grounds along the Barents Sea coast in Northern Russia. This is a well-known model system to study bird migratory timing in relation to the green wave (van der Graaf et al. 2006; Shariatinajafabadi et al. 2014) and climatic variables (Kölzsch et al. 2015). Our study sites are located in preferred feeding salt marsh habitats at three sites along this migratory flyway: one temperate wintering site, one temperate spring stopover site and one Arctic breeding site (Figure 2.1). The first temperate site is situated on the island of Schiermonnikoog in the Wadden Sea, the Netherlands, which is both a wintering and spring staging site for barnacle geese (53°30'N, 6°10'E). The second temperate site is located on the island of Gotland in the Baltic Sea (57°07'N, 18°27'E), a traditional stopover site for migrating barnacle geese in April and May (van der Graaf et al. 2007). The Arctic site is at the Kolokolkova Bay on the Barents Sea coast, northern Russia (68°35'N, 52°20'E), which hosts a breeding colony of barnacle geese (van der Jeugd et al. 2003). Barnacle geese have been breeding in this area since at least 1994 (Syroechkovskiy 1995), and the colony now (2015) comprises approximately 600 breeding pairs (T.L. unpublished data).

Experimental setup

We conducted a warming experiment at our study sites in the spring of 2014 and 2015 to study the effect of warming on forage plants for barnacle geese. At temperate sites we specifically studied Red Fescue (*Festuca rubra*) and at the Arctic site we studied Hoppner's Sedge (*Carex subspathacea*). The use of different plant species on different sites could pose a confounding factor, as differences between sites could alternatively be explained by the differences between species. However, by studying the main forage plants for barnacle geese for these specific sites (van der Graaf 2006; van der Graaf et al. 2006; van der Graaf et al. 2004), we are able to study the effect of warming in the context of goose migration timing rather than to gain a specific understanding of the effects of warming on vegetation at different latitudes. We experimentally warmed vegetation plots at small scale using hexagonal open top chambers (OTC's) with a basal diameter of 208 cm, a height of 50 cm and a side angle of 60°, made from LEXAN polycarbonate (non UV-resistant; Figure 2.1). Our open-top chambers were constructed according to the protocol for the International Tundra Experiment (ITEX) program, which are used in many studies of climate warming (Bokhorst et al. 2013; Marion et al. 1997; Elmendorf et al. 2012; Molau & Edlund 1996). Open-top chambers typically warm the soil temperature with 1 – 3 °C (Molau & Edlund 1996; Marion et al. 1997), which is line with expected

climate warming in this century (Stocker et al. 2013). For every warmed plot we placed a control plot at 1 m distance, which was fenced with chicken wire (1 cm mesh size, 50 cm in height) to prevent geese and other herbivores from entering the plot (Figure 2.1). Five open top chambers and five control plots were placed with at least 50 m distance on each study site for two months during the growing season when the geese were preparing for migration (March – April; Schiermonnikoog), staging on a stopover site during migration (April – May; Gotland) or nesting / rearing offspring on the breeding grounds (early/mid-June – early/mid-August; Kolokolkova Bay, see Table S2.1 for exact dates). Plots were placed in low – middle saltmarsh where forage plant abundance exceeded 50% cover (van Wijnen et al. 1997; van der Graaf et al. 2007; Van Der Graaf et al. 2004). In 2015, plots were placed at least 50 m from locations used in 2014 to avoid repeated measuring on the same plot. In the Kolokolkova Bay the experiment was set up after disappearance of sea ice from the saltmarsh, which was 10 days earlier in 2015 compared to 2014. This could have caused differences between years in the amount of warmed days to which the experimental plots were exposed, which in turn could affect measured parameters. We expect that the general pattern between sites would not be affected.

Data collection

Vegetation

Every 14 days, we 1) counted the density of living green tillers of the forage plants (individual sprouts consisting of 1 – 3 leaves) and 2) collected individual tillers using pairs of tweezers, both in randomly placed 5x5 cm surface squares (2014: 10 squares, 3 tillers collected per square; 2015: 5 squares, 5 tillers collected per square). Measurements were almost always conducted on a single day, and otherwise on (up to three) consecutive days. To reduce the time it took to conduct the measurements, we adjusted the measurement protocol in 2015 to count less squares. We tested that when counting 5 squares, all counts values would fall within the confidence intervals of the original counts using 10 squares (Figure S2.1). We simultaneously increased the number of collected tillers per square in order to collect enough biomass for determining nitrogen concentrations. Once a square was used for data collection it was excluded for the remainder of the experiment. After collection tillers were dried at room temperature and thereafter stored in paper bags for 1 – 2 months. Samples were re-examined in the lab to remove soil particles and dead material, after which they were oven dried at 60 °C for 48 hours, and weighed to the nearest milligram. Samples were then grinded to 1mm particles using a bead mill with steel beads (QIAGEN TissueLyser II), after which nitrogen (N) and carbon (C) content (% of dry weight) were determined on 3-5 mg powdered material in 6 mm diameter metal cups, using a C:N analyser (Flash EA 1112 analyzer from Thermo Fisher Scientific Inc. Waltham, USA). We determined total above ground biomass (dry weight in g m^{-2}) by multiplying the average tiller weight with average tiller density count per square,

multiplying by 400 as we measured in 5x5 cm squares. We combined the measures of above-ground biomass and N concentration to calculate total above-ground nitrogen (in g N m^{-2}). We placed temperature loggers (Ibutton Thermochron 1922L) in the centre of each plot, 2 cm below the surface, which measured soil temperature every 24 min at 0.1 °C accuracy. For every site, the loggers recorded temperature from the day of the first measurements until the day of the last measurement.
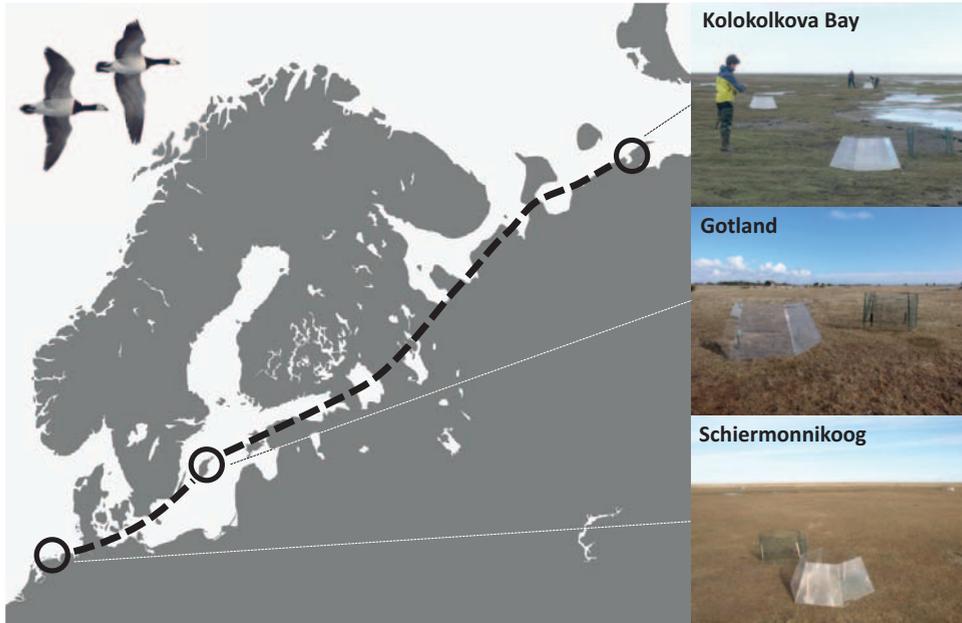
Figure 2.1: Our study sites (black circles) along the spring migration route of the Russian barnacle goose population (black dashed line). Dotted lines connect to photographs of the study sites showing the experimental set-up, with the experiment plots covered by open-top chambers and fenced control plots. Photographs were taken in April 2015 (Schiermonnikoog, photograph by TKL and Gotland, photograph by FJ) and June 2015 (Kolokolkova Bay, photograph by BAN)

Growing degree days

We calculated growing degree days for every year, study site and plot using a combination of the temperature data collected in our plots and temperature data from nearby weather stations. We used the daily mean air temperature data from 2014 and 2015 of the weather station located closest to each study site (Lauwersoog; 8.2 km from Schiermonnikoog, Visby: 58.8 km from Gotland site, Naryan-Mar / Konstantinovsky: 121.8 / 107.1 km from Kolokolkova Bay site; more information in Supplementary materials). We acquired these temperature data from national weather services and from the Russian weather site 'RP5' (KNMI; Swedish Meteorological and Hydrological Institute; www.rp5.ru). To acquire

mean daily temperature specifically for each study site and plot for the entire years 2014 and 2015, we used mean daily temperature data from our plots and added data from weather stations for the months outside the experiment. For the complete dataset we calculated growing degree days (GDD) according to van Wijk et al. (2012), using 0 °C as a threshold temperature for grass growth (Gallagher 1979).

Statistics

We calculated the daily mean and maximum temperature per plot, treatment, and site and tested the effect of our warming treatment by running linear mixed models using the package "*lme4*" in R 3.0.2 (R Development Core Team 2014). We fitted plot as a random factor and included fixed factors treatment, site, year and the interactions between treatment and year and treatment and site. We fitted treatment, year and site as fixed factors and plot (nested in site and year) as a random factor.

We tested the effect of warming on above ground biomass (g m²), nitrogen concentration (%) and above ground nitrogen (g m²) by running linear mixed models. We fitted plot (nested in site and year) as random factor in our models, and included multiple fixed effects, including: days (since start of the experiment), the quadratic term of days, year, site, warming treatment, the interaction between warming treatment and days and an interaction effect between days and site. In models including the fixed factor of treatment we tested whether the treatment led to an increase or decrease in biomass or nitrogen, while in models including the interaction between treatment and days and the quadratic term of days, we tested whether the treatment advanced or delayed the peak value of biomass or nitrogen. Models with combinations of variables were compared using Akaike's Information Criterion (AIC$_c$; Burnham & Anderson 2002) and we chose the model with the lowest AIC$_c$ value as our final model. We tested for significance of fixed factors by comparing the final model with a reduced model in which the fixed factor was absent, using a Likelihood ratio test. As site and the interaction effect of days and site were significant in most models, we tested models separately per site.

Food peak advancement

To investigate the effect of warming on the advancement of food peaks, we additionally conducted an analysis in which we using growing degree days to predict the moment of the food peak under climate warming. Local climate and plant phenology are closely linked (Van der Graaf et al. 2006; Cleland et al. 2007) and peaks in food quality can be predicted by GDD (Botta et al. 2000; Si et al. 2015b). As we advanced the GDD under our warming treatment, we expected food peaks to advance, but only if our treatment affected plant growth. We defined the food peak as the peak in (above ground) nitrogen (g m²) at temperate sites, while for the Arctic site we defined the food peak as the peak

in nitrogen concentration (%), as food requirements differ between adults and chicks, and thus between sites. Food peaks at temperate sites are mostly determined by the combination of high nitrogen concentration and above ground biomass (van der Graaf et al. 2006), facilitating adult geese to rapidly accumulate fat reserves prior to and during migration. The food peak to which geese should time hatching of their eggs in the Arctic is on the other hand determined by the food requirements of the goslings, which should forage on short vegetation, which is high in nitrogen concentration in order to grow fast (Richman et al. 2015; Doiron et al. 2015).

As our treatment only affect plant growth at the Arctic site (see results), we assumed the timing of the food peaks at our temperate sites to be unaffected by climate warming. We calculated the timing of the Arctic food peak by applying the empirically determined polynomial regression between nitrogen concentration (%; NC) and growing degree days (GDD) under climate warming. We determined these relations by running linear mixed models on our experimental data. In our models GDD explained nitrogen concentration better (i.e., lower AIC_c) than days since start of the experiment or Julian days. This relationship did not differ between warmed and control treatments, but differed significantly between years (χ^2 = 40.26, p < 0.001), as we started measuring before nitrogen concentration peaked in 2014 but not in 2015. We included both years in the analysis, as the peak in nitrogen concentration was reached at approximately the same GDD in both years (Figure 2.2). We thus obtained the intercept and the fixed-effects regression coefficients (a, b and c) from linear mixed models including both treatments and both years. This allowed us to create a growing degree day model to calculate nitrogen concentration (NC) for any given Julian day (d) using the GDD of the specific site and day:

$$NC_d = intercept + a(GDD_d)^3 + b(GDD_d)^2 + c(GDD_d) \qquad (2.1)$$

We validated the growing degree day model for nitrogen concentration with data collected in the field (Figure S2.2). We applied the empirically determined relationships to calculate increase of nitrogen concentration under 0.0 – 2.0°C warming, as is this is consistent with the rate of warming in our warming treatment. To calculate the GDD under warming, we first acquired the baseline temperatures from the average temperature per Julian day over the period 2005 – 2015, specific per site (data from weather stations described above). We then added + 1, +1.5 and + 2.0°C to the baseline temperatures. From these temperatures we calculated GDD as described above, and then used these GDD values in formula one and two to calculate nitrogen concentration over Julian days. For every temperature increase we then determined the Julian day at which nitrogen concentration reached its maximum value, which is the 'peak'. We then calculated the advancement of the food peak respective to a the food peak without warming.

Results

Temperature in open-top chambers

The open-top chambers increased the soil temperature in plots on average by 1.0 to 1.7°C for all sites. Both mean and maximum daily temperature were significantly higher in plots warmed by open-top chambers than in control plots (mean temperature: χ^2 = 182.76, df = 1, p < 0.001; maximum temperature: χ^2 = 178.08, df = 1, p < 0.001). The interaction effect of treatment and year was included in the best model for maximum daily temperature, but this was only marginally significant (χ^2 = 2.72, df = 1, p = 0.099). There was no difference in the treatment effect between sites (Table S2.2 and S2.3).
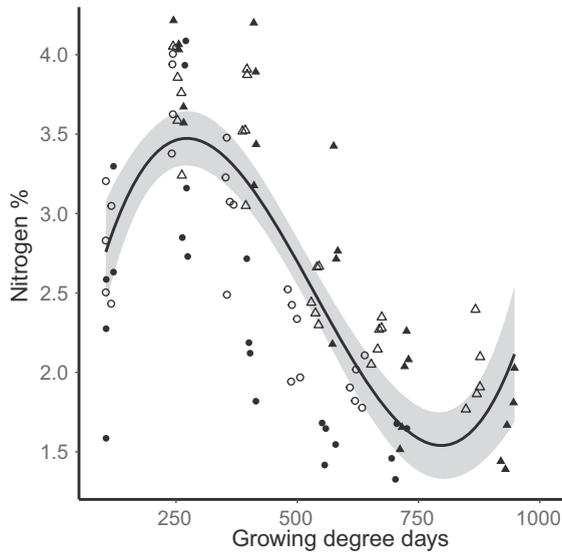
Figure 2.2: Nitrogen concentration (%) over growing degree days (GDD) for the Arctic site. Open symbols represent measurements from the control treatment, closed symbols from the warmed treatment. Circles represent data from 2014, triangles data from 2015. The line show the polynomial regression, with the shaded area representing the 95% CI of the linear functions. Specific regression function: $NC_k = 1.364 + 1.748e^{-02} \cdot GDD_d + -4.305e^{-05} \cdot GDD_d^2 + 2.684e^{-08} \cdot GDD_d^3$ (adjusted R^2 = 0.619).
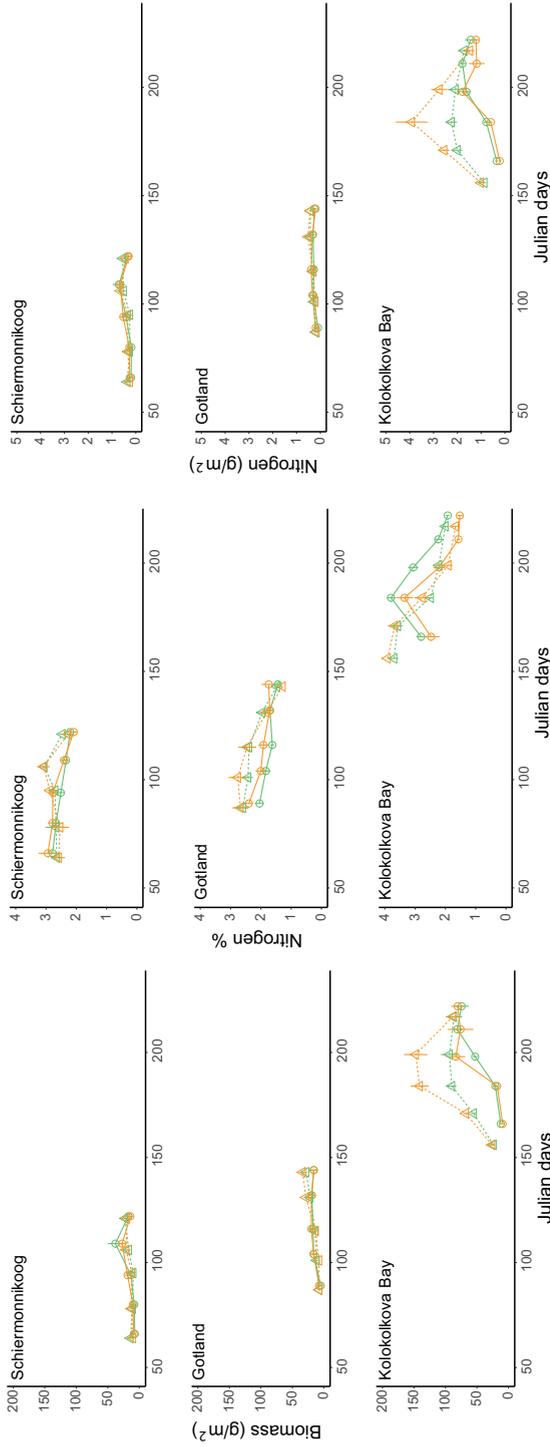
Figure 2.3: Change in biomass (g m²), nitrogen concentration (%) and nitrogen (g m²) over time (in Julian days) of forage plants for both control (green lines) and warmed (orange lines) treatments, in 2014 (circles and solid lines) and 2015 (triangles and dotted lines).

Table 2.1: Significant fixed factors with unstandardixed coefficients in GLMMs run for biomass, nitrogen concentration and above ground nitrogen (g m²).

Test variable	Site	Days	Days^2	Treatment	Year	Days × Treatment	Site	Site × Treatment
Biomass (g/m²)	All	0.967***	-0.008**	1.737**	10.408**		44.829***	12.558*
	Schiermonnikoog	0.367*						
	Gotland	0.416**						
	Kolokollkova Bay	3.750***	-0.039***	14.521**	34.800***			
Nitrogen concentration (%)	All	0.009*	-0.0004***	0.092*	0.299***		0.954***	-0.353*
	Schiermonnikoog	0.012	-0.0003**		0.144			
	Gotland		-0.0003***	0.199	0.362*			
	Kolokollkova Bay		-0.0005***	-0.268*	0.279**			
Nitrogen (g/m²)	All	0.029***	-0.0004***		0.306**		1.246***	
	Schiermonnikoog	0.012*						
	Gotland	0.010**						
	Kolokollkova Bay	0.095***	-0.001***		1.025***			

Asterisks denote significant effects ($p < 0.05$: *; $p < 0.01$: **; $p < 0.001$: ***), italic values denote marginally significant effects. Models for which site is indicated in the second column where run separately for a single site. The variables Site and Site x Treatment were only included in models which were run for all sites.

Warming effects

The effect of warming on plant growth differed between sites and only at the Arctic breeding site Kolokolkova Bay did experimental warming affect forage plant growth and development (Figure 2.3, Table 2.1). Here, the warming treatment was included in the best model for above ground biomass and nitrogen concentration (Table S2.4), in which it was a significant predictor (GLMM: above ground biomass χ^2 = 7.588, p = 0.006; nitrogen concentration χ^2 = 6.300, p = 0.012). In warmed plots, the increase in biomass was significantly higher while the decline in nitrogen concentration was significantly faster. The interaction of the warming treatment and days since start of the experiment was not significant. At the Gotland and Schiermonnikoog sites the treatment effect nor the interaction effect were ever significant (Table 2.1).

Food peak advancement

As our warming treatment did not affect plant growth in our experiment at temperate sites, we assume that timing of temperate food peaks are not affected by the degree of climate warming expected in the coming century. At the Arctic site, our growing degree day analysis predicted the food peak in nitrogen concentration to advance by 4, 5 and 7 days under +1.0, +1.5 and +2.0˚C warming, respectively.

Discussion

We found that experimentally increasing temperatures had a strong effect on forage plants of barnacle geese at our Arctic site but not at the two temperate sites. At the Arctic site, warming resulted in an increase in the peak of biomass and faster decline of nitrogen concentration, whereas warming had no such effects at the temperate sites. Under a 1 to 2 ˚C climate warming, food peaks are unlikely to advance at temperate sites, while food peaks at the Arctic site are predicted to advance up to 7 days.

Effects of experimental warming in the Arctic

The increase of 1.0 – 1.7ºC in our warmed treatment did not differ between sites or years, and were in line with other studies using ITEX open-top chambers in similar climatic regions (Marion et al. 1997; Doiron et al. 2014; Rustad et al. 2001). In our Arctic site, aboveground biomass accumulated faster and to a higher peak level in warmed plots, while nitrogen concentration in the shoots was lower. This is consistent with other experimental warming studies on graminoids in the Arctic region (Doiron et al. 2014; Jónsdóttir et al. 2005). Plants in Arctic regions have in general been found to be more responsive to increased temperatures in summer (Havström et al. 1993; Wal & Stien 2014). Warming, either experimental or natural, will have proportionally larger effects in Arctic regions compared to temperate regions due to colder average temperatures and

can result in prolongation of the growing season (Wal & Stien 2014), which is otherwise inhibited by low summer temperatures (Atkin et al. 2005). A seasonal decline of nitrogen concentration occurs simultaneously with increasing aboveground biomass, a pattern generally found in Arctic plants as they age (Chapin III et al. 1975; van der Graaf et al. 2006; Lepage et al. 1998). The accelerated decline of nitrogen under experimental warming could be a dilution effect which occurs during a simultaneous increase in carbon-rich plant tissues as plant productivity is increased (Doiron et al. 2014; Tolvanen & Henry 2001; Day et al. 2008), although we do not find carbon concentration to be increased in warmed plots. Finally, as previously suggested by Doiron et al. (2014), warming appeared to increase aboveground nitrogen and thus the height of the food peak, although this was not significant. The amplified effect of warming at Arctic sites is in line with results from other studies: meta-analyses report greater positive effects of warming on plant productivity in colder regions (Elmendorf et al. 2012; Rustad et al. 2001).

Food peak advancement

The interaction of days since start of the experiment and the warming treatment was never significant for any of our sites, suggesting that the warming treatment did not advance the moment peak food availability, either in nitrogen (g m^2) or nitrogen concentration. The detection of small advancements in timing of the food peak under experimental warming might however be weakened by differences in the height of the food peak between years and treatments and the low frequency of our measurements (i.e. once every 14 days). When we use our growing degree day model, we predict food peaks to advance 7 days in the Arctic under a 2°C climate warming. Contrastingly, food peaks are unlikely to advance at temperate sites under warming up to 1.7 °C, as out warming treatment did not affect plant growth. The largerwarming response of Arctic forage plants which we find can more strongly advance peaks in food availability further along the migratory flyway, and thus give rise to mismatches between bird migration and peak food availability (Kölzsch et al. 2015; Meltofte et al. 2007; Doiron et al. 2015).

Disruption of the green wave

We find that a temperature increase of 1.0 to 1.7°C had an larger effect of forage plants growth in the Arctic, leading to a stronger increase of biomass and a stronger decline of nitrogen concentration in plants. This can be problematic for small goslings, which cannot access tall grass swards and need short, nitrogen-rich grass for rapid growth after hatching (Doiron et al. 2014; Richman et al. 2015). In the breeding grounds of barnacle geese, climate warming is expected to result in a shorter 'food-peak' during which this high quality forage is available. When goslings feed on lower quality forage after the food peak, they suffer from reduced growth (Doiron et al. 2015; Lepage et al. 1999) and a shorter food peak could thus strongly reduce gosling growth and survival, as has been

found for Arctic-nesting Sanderlings (Reneerkens et al. 2016). At temperate wintering and staging sites experimental warming did not affect forage quality, and fat deposition rates of adult geese preparing for spring migration is thus unlikely to change under climate warming. If the departure date from staging sites is triggered by a seasonal decline in fat deposition rate (Prop et al. 2003), geese would not advance their migration timing in temperate regions under climate warming.

In addition, under a 2°C we predict an advancement of the food peak at the Arctic site but not at temperate sites. A similar climate warming might thus shorten the period between food peaks in the temperate wintering area and the Arctic breeding area. Under a shortening of this period, geese might not have the time to both exploit temperate food peaks prior to migration and still arrive on the breeding grounds on time (Meltofte et al. 2007). Also, as geese time their spring migration according to peaks of nitrogen (van der Graaf et al. 2006), the lack of advancement of food peaks in temperate regions could deteriorate the ability of the geese to predict food conditions on the Arctic breeding grounds (Kölzsch et al. 2015). Either one or the combination of these effects is likely to result in a mismatch between goose migration phenology and peak food availability (Dickey et al. 2008), which has been shown to strongly reduce gosling growth (Doiron et al. 2015). In combination with a shortened food peak in the Arctic the negative effects on gosling growth will be amplified.

Under Arctic amplification the temperature rise in the Arctic is predicted to be 2.2 to 2.4 times higher than the global average (Serreze et al. 2009; Stocker et al. 2013). In addition, high inter-annual variability of the Arctic climate can cause extreme early springs in some years (Gauthier et al. 2013), during which a shortening of the Arctic food peak is likely to occur. Under amplified Arctic warming, the period between food peaks will be shortened even more, increasing the chance of mismatched migration phenology of geese.

Conclusions

To study the effects of climate warming on migratory organisms, spring phenology of their breeding areas has to be seen in connection to their wintering and staging areas along the migratory flyway (Emmenegger et al. 2016). From this viewpoint, we show that climate warming can have a strong deteriorating effect on forage quality in the Arctic breeding grounds, potentially reducing gosling growth, but will not affect forage quality on temperate wintering grounds for staging adult geese. In addition, an advancement of the food peak in the Arctic but not at temperate sites can disrupt the timing between food peaks along the migratory flyway in our study system, which can cause goose migration phenology to become mismatched, particularly considering the Arctic warms faster than the temperate regions (Stocker et al. 2013). The combined effect of a mismatched food peak which becomes shorter as the climate warms, will likely have strong impacts on

goose reproductive success under climate warming by reducing growth and survival of goslings after hatching.

Acknowledgements

Supplementary material
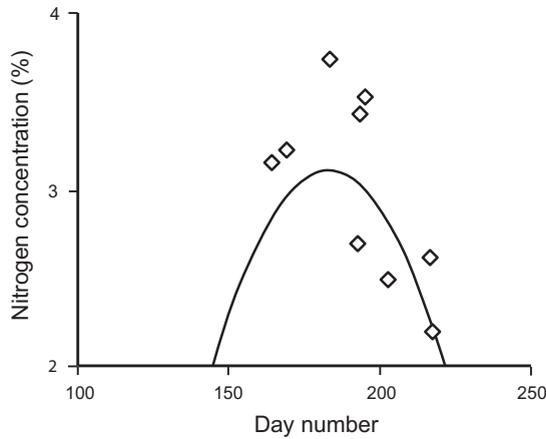
1. Temperature data

We acquired temperature data from weather stations located closest to our study sites. For the Schiermonnikoog site this was the weather station of Lauwersoog (data from Royal Netherlands Meteorological Institute; www.knmi.nl), located 8.2 km from our study site. For the Gotland site this was Visby, Gotland (data from Swedish Meteorological and Hydrological Institute; www.smhi.nl) located 58.8 km away from our study site (Grotlingbo-udd). For the Kolokolkova Bay site we gathered temperature data from two weather stations (data from Raspisaniye Pogodi Ltd: www.rp5.ru and the all-Russian scientific institute for hydro-meteorological information: www.meteo.ru), as these were either located far away from the study site (Cape Konstantinovsky, 121.8 km) or further away from the coast than our study site (Naryan-Mar, 107.1 km) which could be of influence for the temperature. For all sites we checked whether daily average temperature measured by the weather station matched the daily temperature measured by our Ibuttons at the study site during the period of study. At the Kolokolkova Bay site differences were often large (>2°C) and we used the average of both weather stations to create a closer match.

2. Validation of growing degree day model

We validated our growing degree day model on nitrogen concentration for our Arctic study site using data gathered by SvdG on nitrogen concentration in *Carex subspathacea* in 2003 at out Arctic study site in the Pechora delta (van der Graaf et al. 2006). We used temperature data as collected on the study site between 7th of June and 1st of August, which we complemented with temperature data from weather stations as described above. From these temperature data we calculated growing degree days and used our model to calculate nitrogen concentration for every Julian day. We compared the moment of the nitrogen concentration food peak as predicted by our model and as measured at our study site. The model predicted the food peak to occur at day 188 (7th of July), while the highest nitrogen concentration was measured at day 184 (3th of July; Figure S2.2).
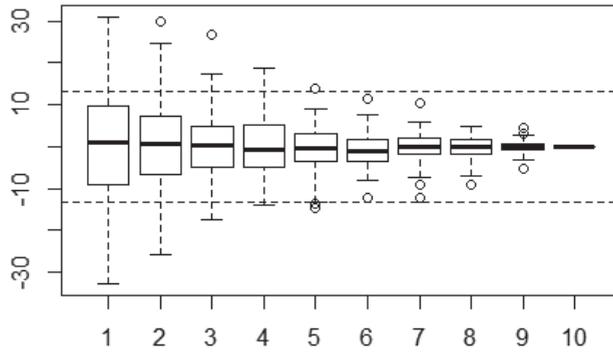
Figure S2.1: Boxplots of the average count values when using 1 to 10 squares for counting. Horizontal dotted lines delineate the 95% confidence intervals of the counts when using 10 squares.

Figure S2.2: Comparison of our growing degree day model in nitrogen concentration at the Arctic site (line) for temperature data from 2003, compared with actual data on nitrogen concentration in *Carex subspathacea* (diamonds).

Table S2.1: All measurement moments during the experiment for all sites and both years 2014 and 2015. The experimental set-up was put up at the day of the first measurement (moment 1) and taken down after the last measurement (moment 5).

Measurement moment	Site & year					
	Schiermonnikoog		*Gotland*		*Kolokolkova Bay*	
	2014	*2015*	*2014*	*2015*	*2014*	*2015*
1	7 March	5 March	30 March	28 March	15 June	5 June
2	21 March	19 March	12 April	11 April	3 July	20 June
3	4 April	5 April	26 April	25 April	17 July	3 July
4	19 April	16 April	10 May	11 May	30 July	18 July
5	2 May	1 May	24 May	23 May	10 August	5 August

Table S2.2: Mean, maximum and minimum daily differences in Celsius degrees between warmed and control treatments, separated for year and location.

	2014			2015		
	min	**mean**	**max**	**min**	**mean**	**max**
Schiermonnikoog	0.87 ± 0.45	1.04 ± 0.14	1.30 ± 0.56	1.13 ± 0.70	1.32 ± 0.21	1.90 ± 0.97
Gotland	1.10 ± 0.45	1.68 ± 0.51	2.90 ± 1.26	0.60 ± 0.36	1.37 ± 0.27	2.00 ± 0.84
Kolokolkova Bay	0.87 ± 0.51	1.29 ± 0.33	1.80 ± 0.72	0.77 ± 0.58	0.99 ± 0.19	1.50 ± 1.19

Table S2.3: Final GLMMs for mean and maximum temperature with coefficient values for fixed effects. Asterisks denote significant effects (p < 0.05: *; p < 0.01: **; p < 0.001: ***), italic values denote marginally significant effects.

Test variable	Intercept	Site	Treatment	Year	Treatment* Site	Treatment* Year	degrees of freedom	Log likelihood	AICc
Mean temperature	9.837	-0.78**	1.28***				7	-10602.56	21217.1
Maximum temperature	1330.00	-1.26***	865.37***	-0.59***		-0.43	8	-11957.84	23931.7

Table S2.4: Final GLMMs for biomass, nitrogen content and nutrient biomass with coefficient values for fixed effects.

	Intercept	Days since start	Days ^{2}	Treatment	Year	Site	Site × treatment	degrees of freedom	Log likelihood	AIC_c
Biomass										
All sites	-8.729	0.967	-0.008	1.737	10.408	44.829	12.558	11	-1733.56	3489.8
Kolokolkova Bay	-21.3	3.750	-0.039	14.521	34.800			7	-451.48	918.2
Gotland	5.749	0.416	-0.002	1.417				6	-341.03	695.0
Schiermonnikoog	9.049	0.367	-0.002		-1.803			6	355.28	723.5
Nitrogen concentration (%)										
All sites	1.936	0.009	-0.0004	0.092	0.299	0.954	-0.353	11	-275.17	573.1
Kolokolkova Bay	3.314		-0.0005	-0.268	0.279			6	-71.14	155.2
Gotland	2.122		-0.0003	0.199	0.362			6	-433.01	78.9
Schiermonnikoog	2.597	0.012	-0.0003		0.144			6	43.50	100.0
Nitrogen (g/m²)										
All sites	-0.235	0.029	-0.0004		0.306	1.246		8	-224.04	464.5
Kolokolkova Bay	-0.149	0.095	-0.001		1.025			6	-86.50	186.0
Gotland	0.126	0.010	-0.0001		0.055			6	63.48	114.0
Schiermonnikoog	0.220	0.012	-0.0001		0.010			6	15.06	-17.1